

A new approach to octopuses' body pattern analysis: A framework for taxonomy and behavioral studies*

Tatiana S. Leite¹ and Jennifer A. Mather²

¹ Universidade Federal do Rio Grande do Norte, Departamento de Oceanografia e Limnologia, Via Costeira s/n, Bairro de Mãe Luiza, Natal/RN, Brazil CEP 59014-100, leite_ts@yahoo.com.br

² University of Lethbridge, Department of Psychology, 4401 University Drive, Lethbridge, Alberta T1K 3M4, Canada, mather@uleth.ca

Abstract: We systematically analyzed octopus body patterns, based on locations of chromatophore nerve projection, using a proposed new species in the *Octopus vulgaris* Cuvier, 1797 complex, *Octopus insularis* Leite and Haimovici, 2008. Although some taxonomic studies have used body patterns as characters to describe octopus species, a systematic analysis would provide detailed descriptions to assist reliable comparisons among species. This approach also links body patterns, behaviors, and underlying physiology of the chromatophore system. Body patterns were characterized by percent occurrence, areas of skin, and number of components in each. To verify the distribution of chromatic components, skin patterns, and colors among areas of the body, we ran a cluster analysis on occurrence of the components. We identified a total of 16 chromatic, 5 texture, 9 skin units, 6 colors, and 9 chronic body patterns. The cluster analysis showed twelve distinct skin areas of the components' distribution (expressive fields). Smaller fields were found in areas with complex patterns, especially around the eyes, while larger ones were found in areas with simple patterns. These findings differentiate between morphological and physiological units of the display system. The strong degree of similarity among photographs also supports previous taxonomic studies that pointed to morphological similarity within this species from the oceanic islands of northeastern Brazil.

Key words: *Octopus insularis*, behavior

The complex and changing appearance of cephalopod molluscs offers a challenge to the biologist, both in description (Packard and Sanders 1969, Hanlon and Messenger 1988) and in linkage of its body display to specific behaviors (Adamo and Hanlon 1996, Hanlon *et al.* 1999a, Mather and Mather 2004, Adamo *et al.* 2006). Many authors (Packard and Sanders 1969, Packard and Hochberg 1977, Hanlon and Hixon 1980, Hanlon and Messenger 1988, Roper and Hochberg 1988, Mather and Mather 1994, Hanlon *et al.* 1999b) have constructed a repertoire of the body pattern behavior either for one species or to discriminate among species. The problem of species identity is particularly difficult in the *Octopus vulgaris* Cuvier, 1797 species complex (Mangold and Hochberg 1991, Mangold 1998, Söller *et al.* 2000, Warnke *et al.* 2004). Morphological and morphometric analyses have suggested the occurrence of *Octopus insularis* Leite and Haimovici, 2008 (Leite *et al.*, 2008), a cryptic species of this complex from the northeast of Brazil (Leite and Haimovici 2006, Leite 2007), and cataloging body patterns may be a useful addition to separate it from other species and to compare conserved characters (Hanlon 1988, Hanlon and Messenger 1996). Such information can be gained from careful analysis of patterns taken from underwater photographs and

film. Recent analysis of films of *Sepia officinalis* Linnaeus, 1758 has used Bayesian probability to identify pattern (Crook *et al.* 2002), Independent Component Analysis to delineate the basic components (Anderson *et al.* 2003), and Principal Components Analysis to look for camouflage units (Kelman *et al.* 2007). Multivariate analyses can also be used to assess symmetry of body pattern expression (Langridge 2006) to understand camouflage (Kelman *et al.* 2007) or to aid in species differentiation, as in the present study.

Body pattern is composed of chromatic, textural, and postural components that combine to produce the final appearance of the individual (Hanlon 1988). Body patterns are controlled at several levels, and chromatophores are the most important elements that define chromatic components. The chromatophores, organized on the body surface into groups designated as "morphological" and "physiological" units, are the smallest units (Packard 1974). The morphological unit is a static arrangement of chromatophore density in the skin, such as patches and grooves, while the physiological units are a dynamic event, resulting from neural activation of a particular set of nerves in a specific area (Messenger 2001). These areas are called "motor fields" or "chromatophoric fields" (Packard 1974, Messenger 2001)

* From the symposium "Cephalopods: A behavioral perspective" presented at the joint meeting of the American Malacological Society and Western Society of Malacologists, held 29 July to 3 August 2006 in Seattle, Washington.

and are usually irregular with overlapping boundaries (Packard 1974). These chromatophoric fields depend both on the distribution of chromatophores in the skin and organization of their neuromotor control (Messenger 2001).

Because chromatophores are innervated directly from the brain, it should be possible to map the projection of the chromatophore nerves onto the body surface to describe the larger units that Messenger (2001) calls "chromatomotor fields." Froesch (1973) found 20 areas of projection of chromatophore nerves on the body surface when he made selective lesions in *Octopus vulgaris*, and Bühler *et al.* (1975) divided the mantle into 23 smaller projection areas, based on 40 nerves leaving the stellate ganglion.

We believe that using photos of living octopus to analyze body patterns systematically, based on locations of chromatophore nerve projection on the body surface would make it possible to link body pattern components to areas of nerve projection, as well as linkages to behavior states. Body patterns were characterized in percentage of occurrence, locations and numbers of components, and cluster analyses were used to identify groups of similarities among photographs and among octopus body surfaces.

MATERIALS AND METHODS

Juvenile and adult specimens of *Octopus insularis* from the Fernando de Noronha Islands, a northeastern Brazilian oceanic archipelago (03°51'S, 32°25'W) located 345 km northeast of Cape San Roque, Brazil, were photographed from 1999 to 2005, during walking trips near shore, snorkeling, and scuba diving. They were found at a depth of 0.1 to 25 m, in areas of rock, rubble, and small sand patches, with water temperature ranging from 23 to 27°C. We ob-

tained 365 photographs with a digital Canon Power Shot and Sony S50, both 5.0 megapixel, from 93 octopuses.

Conspicuous characteristics of body patterns, behavior, and habitat were used to exclude photographs of three other species of Octopodidae from the analysis: *Octopus hummelincki* Adam, 1936 was identified by the ocellus below the eyes; *Octopus defilippi* Verany, 1851, found only on sand and mud in the Rocas atoll, was identified by the white-cream color; and *Callistoctopus macropus* Risso, 1826, a nocturnal species, could be easily identified by conspicuous white spots all over the body. All photographs without the characteristics cited above but with characteristics common to *Octopus vulgaris* (Nesis 1987, Voss and Toll 1998) were classified as *Octopus insularis*. A subset of photographs was chosen based on an *a priori* assessment of image quality, definition, portion of the body visible, and body pattern. We chose 65 photographs from 23 animals that showed at least three areas of the body (e.g., mantle, head, and at least one arm), were of high quality, and were not the same pattern, date, and individual. We determined different behaviors, body patterns, and their relationships based on Packard and Sanders (1971), Roper and Hochberg (1988), and Hanlon *et al.* (1999a), plus the components (chromatic, textural, colors) and skin patterns present in each photograph (Tables 1-2). The components and skin pattern were catalogued based on Packard and Sanders (1969), Roper and Hochberg (1988), and Mather and Mather (1994) (Table 2). The colors were the five cited by Messenger (2001) for *O. vulgaris*, plus Blue-Green, derived from the iridophores (Florey 1966, 1969, Messenger 1974, Cooper *et al.* 1990).

Presence of components and colors throughout the body and within each body pattern

We analyzed the photographs for presence or absence of each chromatic and textural component, color, and skin

Table 1. Behavior states and the chronic body patterns identified in photographs of *Octopus insularis* from Fernando de Noronha, Brazil.

	Definition	Acronyms	References
Behavior states	Inside Den	D	
	Outside Den	OUT	
	Hunting	H	
	Swimming	S	
	Mating	M	
Body patterns	Blotch-light blotch and spots spread throughout more than 50% of the skin surface	BL	see chronic Mottle pattern in Hanlon <i>et al.</i> (1999)
	Dymantic	D	Packard and Sanders (1971)
	Dorsal Light-Ventral Blue-Green	DL-VBG	see counter-shading pattern in Hanlon <i>et al.</i> (1999)
	Mottle	M	see Packard (1969)
	Uniform Dark	UD	see Flush in Roper and Hochberg (1988)
	Flamboyant	F	variation of Packard and Sanders (1971)

Table 2. Components (chromatic, texture, and skin pattern) determined from photographs of *Octopus insularis* from Fernando de Noronha, Brazil (based on Packard and Sanders 1969, 1971, Mather and Mather 1994). R, restricted to specific body area.

Components		Acronym
Chromatic	Alternate bands (light/dark)	ABA
	Alternate light/dark around the eye (R)	ABE
	Brown-yellow blotch	BB
	Blue-green around the eye (R)	BGE
	Black hood	BH
	Dark bar across the eye (R)	DBE
	Dark blotch above eye (R)	DBA
	Dark spots	DS
	Longitudinal dark strip	LDS
	Light blotches	LB
	Purple around suckers (R)	PS
	Red bar across the eye (R)	RBE
	White bar across eye (R)	WBE
	White spots	WS
	White dots	WD
	White V (R)	WV
Textural	Big papillae (>1 cm)	BP
	Small papillae (<1 cm)	SP
	Smooth skin	S
	Rugose skin	R
	Textured skin (skin with a large number of small papillae)	T
Skin pattern	Alternate bands	AB
	Bars	BR
	Blotch	BL
	Dark smooth	DS
	Light smooth	LS
	Reticulate dark	DR
	Reticulate light	LR
	Reticulate mixed (dark and light)	R
Colors	Red/white reticulate	RWR
	Yellow	Y
	Red	R
	Brown	B
	Black	BL
	White	W
	Blue-green	BG

pattern on forty-nine parts of the body (Fig. 1A). These body parts were delineated based on the projection of chromatophore nerves onto the body surface (Froesch 1973, Bühler *et al.* 1975), plus additional divisions in the areas that were much too large, such as mantle and arms (Fig. 1A). Classification of the arms position followed Mather (1998), with the right and left arms numbered: 1st, 2nd, 3rd, and 4th (corresponding to the areas 7, 8, 9, and 10). Within a single arm,

the proximal areas were categorized as 1 and 2 and the distal areas, 3 and 4.

To verify occurrence and area of each component and color throughout the body, we calculated: (the number of areas in which a component appeared in the photograph analyzed)/(total areas of body analyzed in the photograph) $\times$ 100. For example, the Dark bar in the eye (DBE) occurred in two areas of the body and we analyzed 30 areas in this photograph, so the occurrence for this component would be $(2/30) \times 100 = 6.7\%$ (see Appendix 1 for details). We considered that components with 80% or more occurrences in an area could be considered typical for this area, and with 50-80% could be considered common for it.

To verify the distribution of chromatic components, skin patterns, and colors among the areas of the body, we ran a cluster analysis based on occurrence of all these components, except Brown and White, throughout the areas. These two colors were not considered because they were found throughout the body.

Typical and common components for the body patterns and species

To verify the degree of relationship that each component, skin pattern, and color had with each body pattern, we determined the mean occurrence of each component for the main body patterns: Mottle, Blotch, Uniform Dark, Dynamic, and Dorsal Light-Ventral Blue-Green. We calculated: (the times that each component appeared in the photographs within a distinct body pattern)/(total of photograph analyzed with this body pattern) $\times$ 100. For example the DBE appeared in 5 of 10 photographs classified as Uniform Dark, so the occurrence for this component would be 50% in this body pattern. If a component appeared only in areas of the body that were not present in the photograph analyzed, the photograph was not included in the total.

We considered that components with 80% or more occurrences in all body patterns could be considered "typical" for the species and with 50-80% could be considered "common" for this species (Appendix 2). The components with $\geq 80\%$ or more only in one body pattern were considered typical for them; those with 50-80% were considered common.

Similarity among photographs

To determine how many groups of animals could be differentiated from the photographs, a cluster analysis was run, taking into account the presence and degree of expression of each component throughout the parts of body. A cluster analysis encompassed a number of different classification algorithms to join together objects (photographs and skin areas) in successively larger clusters, using some measure of similarity or distance (Statistic Program Contents 2000). A typical result of this type of clustering was a hier-



Figure 2. Six body patterns, seven chromatic, and two textural components identified in photographs of *Octopus insularis* from Fernando de Noronha, Brazil: A, Mottle; B, Blotch; C, Dymantic; D, Dorsal Light-Ventral Blue-Green; E, Uniform dark; and F, Flamboyant. WV, white V spot in the middle of the dorsal head; BGE, Blue green around the eyes; ABA, Alternate bars on arm; DBE, Dark bar across the eye; ABE, Alternate bars across the eye; BH, Black hood on mantle; PS, Purple around suckers; BP, Big papillae; and SP, Small papillae.

five of more than one. The analysis showed clustering among all lateral areas of the mantle (1L1, 1L2, 1L3, and 1L4), among two areas of the head (4V and 6V), among distal parts of the 1st, 2nd, and 3rd dorsal arms (7D3, 7D4, 8D3, 8D4, 9D3, and 9D4), proximal parts of 1st, 2nd, and 3rd

dorsal arms, including 7D1, plus dorsal mantle 1D (7D2, 8D1, 8D2, 9D1, 9D2, and 1D), and among the ventral mantle and ventral parts of 1st, 2nd, 3rd, and 4th arms, plus the dorsal part of the 4th arms (1V, 7V, 8V, 9V, 10D, and 10V). The areas 10D1 and 10D2 were not considered in the analysis because it was not possible to see them in any photograph. Dorsal areas showed a larger number of components (7-10) than ventral arms and mantle did (4).

Typical components, skin pattern, and colors for the body patterns and species

The analysis of occurrence of the chromatic component, skin pattern, and colors for the five common Body Patterns (Mottle, Blotch, Uniform dark, Dymantic, and Dorsal Light-Ventral Blue-Green) allowed us to show that some components were typical to the species or the body pattern. Typical components of the species were Purple Edge on Suckers (<87.5%), Dark Bar Across the Eye (85%), and Red/White Reticulate on ventral arms (100%) (Appendix 2). Other components considered common to the species were: paired white mantle spots (1D) (61%), frontal white V (7D1), blue green around the eyes (3, 4D, and 6D), and alternate arm bars (all >50%).

Only Blotch and Mottle had typical components (>80%). The typical chromatic components for Blotch were Dark Bar across the Eye (DBE), Light Blotch (LB), Blue-Green around the Eye (BGE), and Purple Suckers (PS); for Mottle, they were DBE, White Spots (WS), White Frontal V (WV), Alternate Bands on Arms (ABA), and Purple Suckers (PS) (Appendix 2 and Fig. 2).

Similarity among photographs

The cluster analysis indicated that the photographs formed one large similar group (Fig. 4). This analysis showed similarity among the pictures, based on occurrence of the components throughout areas of the body, despite

Table 3. Occurrence of the six chronic body patterns at the behavior states identified from photographs of *Octopus insularis* ($N = 65$) taken at Fernando de Noronha.

Behavior states/ body pattern	Outside den	%	Inside den	%	Hunting	%	Swimming	%
DL-VBG	2	15.4	0	0.0	0	0.0	5	45.5
Mottle	3	23.1	4	36.4	14	60.9	0	0.0
Blotch	6	46.2	0	0.0	3	13.0	1	9.1
Dymantic	2	15.4	3	27.3	1	4.3	1	9.1
Uniform dark	0	0.0	4	36.4	4	17.4	4	36.4
Flamboyant	0	0	0	0	1	4.3	0	0

differences among Body Patterns, which probably indicated that the specimens belonged to the same species. The cluster analysis just separated three pictures with conspicuous patterns and proportion of components from the larger group: Flamboyant and two pictures of Uniform Dark during Swimming.

DISCUSSION

Body patterns are a useful taxonomic characteristic for identifying cephalopods in the natural environment (Moynihan 1975, Hanlon 1988, Hanlon and Messenger 1996). This study supports this statement using quantitative analyses as well as qualitative ones to analyze body patterns. Although components had different areas of occurrence and degrees of expression, these parameters were uniform enough that almost all pictures were considered similar by cluster analysis. This strong degree of similarity among the pictures classified as *Octopus insularis* from Fernando de Noronha supports previous taxonomic studies that pointed to morphological similarity in this species (Leite and Haimovici 2006, Leite 2007).

Although qualitative analyses are sometimes not enough to distinguish species or subspecies, they can be used as an indicator. A comparison of body patterns of *Octopus insularis* with ones described for *Octopus vulgaris* from the Mediterranean (Packard and Sanders 1969, 1971) and Bermuda (Mather and Mather 1994) showed that some chromatic and textural components occurred in both species. These are frontal white spots (forming a "V" in *O. insularis* and split for *O. vulgaris* from the Mediterranean) (Fig. 2B), mantle white spots (not described for *O. vulgaris* from Bermuda), arm bars, eye bar, black hood, and long papillae on the mantle and head. Otherwise some components such as the extended hood and transverse stripes (chevron), eye ring, head bar mantle shield, and grainy texture were observed for *O. vulgaris* only from the Mediterranean. Some components described in this study for *O. insularis*, such as blue-green around the eye (Fig. 2A) and alternate light and dark around

the eye (Fig. 2B), had not been cited for *O. vulgaris* from either region.

The quantitative results showed that only a small number of components can always be observed across different body patterns. These results make it difficult to do a general Body Pattern description for this species, such as that of *Haplochlada maculosa* (Hoyle, 1883) (Roper and Hochberg 1988). However, some components were strongly related to specific body patterns, and this close relationship was useful to make a solid characterization of the body patterns that will be useful in future research.

Simple body patterns are found in cephalopods with fewer and larger chromatophores, which could generate fewer components, and complex body patterns are found in species with many and small chromatophores, which could generate more components (Messenger 2001), but this may vary within species. Simple and complex body patterns may, therefore, depend on the number of components. The complex ones (e.g., with more components) were observed during Hunting and Outside Den (Blotch and Mottle), while the simpler ones (fewer components) were more common during Swimming (Dorsal Light-Ventral Blue-Green and Uniform Dark). As the octopuses were photographed outside their den in habitats of different complexity including coral reef, bed rocks, and rock shores, the high degree of complexity could be explained if some habitats require complex body patterns to match them. That might be true for *Octopus insularis*, but not for all species: Hanlon *et al.* (1999a) found *Octopus cyanea* Gray, 1849 exhibited little background-matching outside its den. The degree of complexity that body patterns show within the same species or even individual in relation to the environment indicates a great sophistication of pattern use (Messenger 2001) that needs to be evaluated in detail for many species.

Different levels of complexity of distribution can also be found throughout different regions of the body in a single species and may determine the components and patterns that each region can display. During studies of *Loligo opalescens* (Berry, 1911) chromatophores, Florey (1966, 1969)

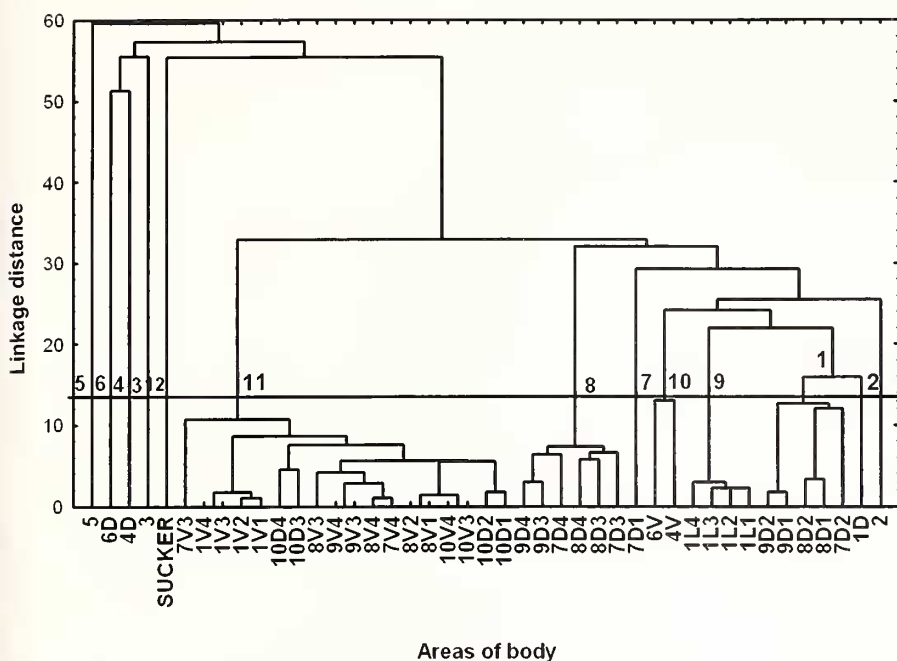


Figure 3. Classification of *Octopus insularis* body skin areas, using cluster analysis. Similarity among body areas was calculated by means of the proportion of occurrence of components, skin patterns, and colors (red, yellow, and blue-green). The line is the cut point, and the numbers indicate twelve different groups of areas on the skin (see Fig. 1B).

found large and sparse chromatophores with single innervation in the ventral mantle, and small and numerous chromatophores with multiple innervations in the dorsal mantle. We also found simple body patterns in ventral areas (mantle and arms) and complex ones in the dorsal areas (mantle, head, and arms). Different degrees of complexity of pattern throughout body areas of an individual can be explained if more complex areas such as the dorsal areas are more visible and vulnerable than others, while less visible areas such as the ventral arms and ventral mantle show simple patterns. Remember, the skin system is widely believed to have evolved as camouflage (Packard 1974).

Differential occurrences of components in different skin areas as defined by Froesch (1973) should have helped us understand the effective projection area of chromatophore fields. When we analyzed the spatial extent of components and patterns, however, we found twelve areas with common patterns that we call “expressive fields” (Fig. 1B). Some of Froesch’s (1973) areas, such as the projection of nerve 5 and 3 at and near the eye, do predict the expressive fields that we found. However, not all of his areas match our findings. For instance, the mantle divides into three large expressive fields, not the large number of projections described by Buhler *et al.* (1975). This important finding reflects the division into different morphological and physiological units which is also

seen at the lower level (Packard 1974, Messenger 2001). Our knowledge of the projection areas for pattern (Messenger 2001) is improved when the areas used are the expressive fields.

Bringing order to a complex system such as expression of body patterns, analyzing them as located in expressive fields, and linking them to different situations has many uses. The first is the possibility of using them as an additional means of species identification (Hanlon 1988, Roper and Hochberg 1988, Hanlon and Messenger 1996) in conjunction with morphological and molecular analyses. Beyond this, a systematic analysis of the locations of components may shed light on the physiology of the complex, chromatophore-control system (Messenger 2001) and discriminate the many levels of motor fields on the skin. Additionally, linkage of specific patterns to behavioral states has been traced only for a few displays such as those of *Sepia officinalis* (Adamo *et al.* 2006) and *Octopus rubescens* Berry,

1853 (Warren *et al.* 1974) during hunting, and the Passing Cloud of *O. cyanea* to startle potential prey (Packard and Sanders 1969, Mather and Mather 2004). With a more systematic analysis, new linkages of behavior and color pattern may become clear. This kind of analysis can thus be the key to accessing the behavioral plasticity and sophisticated neural control that modern cephalopods have developed (Hanlon and Messenger 1996) through evolution.

ACKNOWLEDGMENTS

This research had financial support from the Boticário Foundation of Environmental Protection/Brazil (FBPN). The first author received a scholarship from CNPq (National Council of Scientific and Technological Development) at the Graduate School in Biological Oceanography at the University of Rio Grande and a short term scholarship from CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) to stay at the University of Lethbridge, Canada. We thank the University of Lethbridge for its hospitality in the academic year 2005-2006. The research at the National Park of Fernando de Noronha was possible with an authorization by IBAMA. Professor Jorge Lins at the University of Rio Grande do Norte (UFRN) and the adminis-

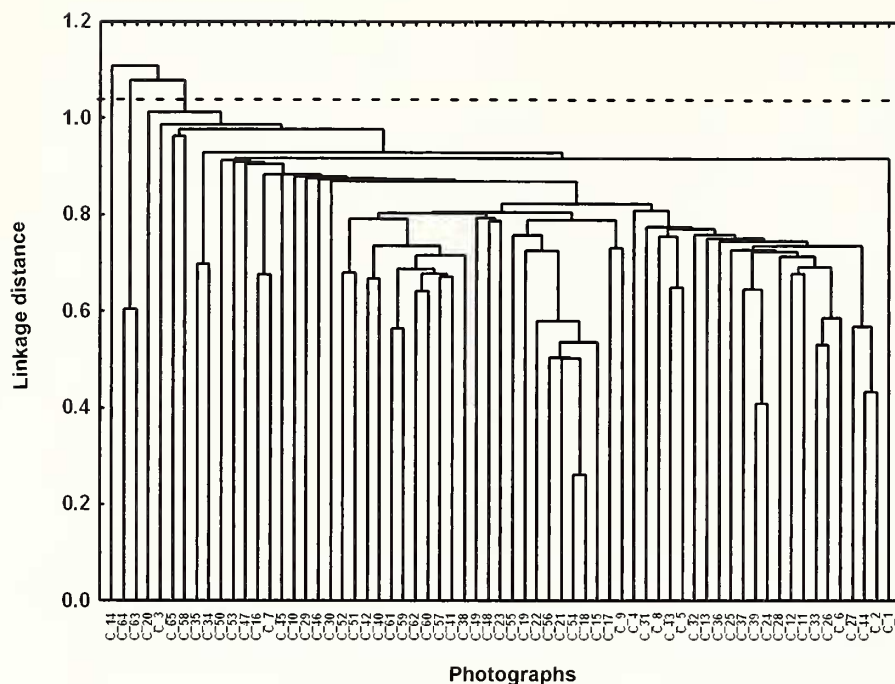


Figure 4. Classification of *Octopus insularis* photographs, using cluster analysis based on the single-linking method. Similarity among photographs was calculated by means of the proportion of the body patterns components through the body (= number of times that components appeared at the areas of the picture/number of areas analyzed).

tration of Fernando de Noronha provided invaluable logistic support. We would like to thank Atlantis Divers, Águas Claras, and Noronha Divers for scuba diving support; Hydrosphera Productions and the underwater photographers: Zaira Matheus, Fábio Guilherme (CQ), Dayse Brisola, Lizandro Almeida, and Diogo Pagnoncelli for the octopus photographs and films made available, John Vokey for his advice on statistical analyses and Ruth Braun for her help and patience with the manuscript revisions. We also would like to thank the volunteers that worked at the Cephalopod Project for their help.

LITERATURE CITED

- Adamo, S. A. and R. T. Hanlon. 1996. Do cuttlefish (Cephalopoda) signal their intentions to conspecifics during agonistic encounters? *Animal Behaviour* **52**: 73-81.
- Adamo, S. A., K. Ehgoetz, C. Sangster, and I. Whitehorne. 2006. Signalling to the enemy? Body pattern expression and its response to the external cues during hunting in the cuttlefish *Sepia officinalis* (Cephalopoda). *Biological Bulletin* **210**: 192-200.
- Anderson, J. C., R. J. Baddeley, D. Osorio, N. Shashar, C. W. Tyler, V. S. Ramachandran, A. C. Crook, and R. T. Hanlon. 2003. Modular organization of adaptive colouration in flounder and cuttlefish revealed by independent component analysis. *Network: Computation in Neural Systems* **14**: 321-333.
- Bühler, A., D. Froesch, K. Mangold, and H.-J. Marthy. 1975. On the motor projection of the stellate ganglion in *Octopus vulgaris*. *Brain Research* **88**: 69-72.
- Cooper, K. M., R. T. Hanlon, and B. U. Budelmann. 1990. Physiological color change in squid iridophores. II. Ultrastructural mechanisms in *Lolliguncula brevis*. *Cell and Tissue Research* **259**: 15-24.
- Crook, A. C., R. Baddeley, and D. Osorio. 2002. Identifying the structures in cuttlefish visual signals. *Philosophical Transactions of the Royal Society of London (B, Biological Sciences)* **357**: 1617-1624.
- Florey, E. 1966. Nervous control and spontaneous activity of the chromatophores of a cephalopod, *Loligo opalescens*. *Comparative Biochemistry and Physiology* **18**: 305-324.
- Florey, E. 1969. Ultrastructure and function of cephalopod chromatophores. *American Zoologist* **9**: 429-442.
- Froesch, D. 1973. Projection of chromatophore nerves on the body surface of *Octopus vulgaris*. *Marine Biology* **19**: 153-155.
- Hanlon, R. T. 1988. Behavioral and body patterning characters useful in taxonomy and field identification of cephalopods. *Malacologia* **29**: 247-264.
- Hanlon, R. T. and R. F. Hixon. 1980. Body patterning and field observations of *Octopus burryi* Voss, 1950. *Bulletin of Marine Science* **30**: 749-755.
- Hanlon, R. T. and J. B. Messenger. 1988. Adaptive coloration in young cuttlefish (*Sepia officinalis* L.): The morphology and development of body patterns and their relation to behaviour. *Philosophical Transactions of the Royal Society of London (B, Biological Sciences)* **320**: 437-487.
- Hanlon, R. T. and J. B. Messenger. 1996. *Cephalopod Behaviour*. Cambridge University Press, Cambridge, UK.
- Hanlon, R. T., J. W. Forsythe, and D. E. Joneschild. 1999a. Crypsis, conspicuousness, mimicry and polyphenism as antipredator defenses of foraging octopuses on Indo-Pacific coral reefs, with a method of quantifying crypsis from video tapes. *Biological Journal of the Linnean Society* **66**: 1-22.
- Hanlon, R. T., M. R. Maxwell, N. Shashar, E. R. Loew, and P. R. Boyle. 1999b. An ethogram of body patterning behavior in the biomedically and commercially valuable squid *Logilope pealeii* off Cape Cod, Massachusetts. *Biological Bulletin* **197**: 49-62.
- Kelman, E. J., R. J. Baddeley, A. J. Shohet, and D. Osorio. 2007.

- Perception of visual texture and the expression of disruptive camouflage by the cuttlefish, *Sepia officinalis*. *Proceedings of the Royal Society (B)* **274**: 1369-1375.
- Langridge, K. V. 2006. Symmetrical crypsis and symmetrical signalling in the cuttlefish *Sepia officinalis*. *Proceedings of the Royal Society (B)*. **273**: 959-967.
- Leite, T. S. 2007. *Taxonomia, distribuição, ecologia alimentar, pesca e opções de manejo de uma nova espécie de polvo* (Octopus insularis: Cephalopoda), no Arquipélago de Fernando de Noronha, Brasil. Ph.D. Dissertation, Fundação Universidade Federal de Rio Grande, Brazil [in Portuguese].
- Leite, T. S. and M. Haimovici. 2006. Presente conhecimento da biodiversidade e habitat dos polvos (Cephalopoda: família Octopodidae) de águas rasas das ilhas oceânicas do nordeste brasileiro. In: R. J. V. Alves and J. W. A. Castro, eds., *Ilhas Oceânicas Brasileiras—da Pesquisa ao Manejo*, vol. 1. Ministério do Meio Ambiente (MMA), Brazil. Pp. 199-214 [in Portuguese].
- Leite, T. S., M. Haimovici, W. Molina, and K. Warnke. 2008. Morphological and genetic description of *Octopus insularis* new species (Cephalopoda: Octopodidae), a cryptic species in the *Octopus vulgaris* complex from the tropical Southwestern Atlantic. *Journal of Molluscan Studies* **74**: 63-74.
- Mangold, K. 1998. The Octopodinae from the Eastern Atlantic Ocean and the Mediterranean Sea. In: N. A. Voss., M. Vecchione, and R. B. Toll, eds., *Systematics and Biogeography of Cephalopods*, vol. II. Smithsonian Contributions to Zoology, Washington, DC. Pp. 521-528.
- Mangold, K. and F. Hochberg. 1991. Defining the genus *Octopus*: Redescription of *Octopus vulgaris*. *Bulletin of Marine Science* **49**: 665.
- Mather, J. A. 1998. How do octopuses use their arms? *Journal of Comparative Psychology* **112**: 306-316.
- Mather, J. A. and L. Mather. 1994. Skin colours and patterns of juvenile *Octopus vulgaris* (Mollusca, Cephalopoda) in Bermuda. *Vie Milieu* **44**: 267-272.
- Mather, J. A. and L. Mather. 2004. Apparent movement in a visual display: The 'passing cloud' of *Octopus cyanea* (Mollusca: Cephalopoda). *Journal of Zoology* **263**: 89-94.
- Messenger, J. B. 1974. Reflecting elements in cephalopod skin and their importance for camouflage. *Journal of Zoology* **174**: 387-395.
- Messenger, J. B. 2001. Cephalopod chromatophores: Neurobiology and natural history. *Biological Reviews* **76**: 473-528.
- Moynihan, M. 1975. Conservatism of displays and comparable stereotyped patterns among cephalopods. In: G. Baerends, C. Beer, and A. Manning, eds., *Function and Evolution in Behaviour*. Clarendon Press, Oxford, UK. Pp. 276-291.
- Nesis, K. N. 1987. *Cephalopods of the World*. T. F. H Publications. Moscow, Russia.
- Packard, A. 1974. Chromatophore fields in the skin of the octopus. *Journal of Physiology* **238**: 38-40.
- Packard, A. and G. Sanders. 1969. What the octopus shows to the world. *Endeavor* **28**: 92-99.
- Packard, A. and G. Sanders. 1971. Body patterns of *Octopus vulgaris* and maturation of the response to disturbance. *Animal Behaviour* **19**: 780-790.
- Packard, A. and F. G. Hochberg. 1977. Skin patterning in *Octopus* and other genera. *Symposium of the Zoological Society of London* **38**: 191-231.
- Roper, C. F. E. and F. G. Hochberg. 1988. Behavior and systematics of cephalopods from Lizard Island, Australia, based on color and body patterns. *Malacologia* **29**: 153-193.
- Statistic Program Contents. 2000. Computer program manual. StatSoft, Inc. Tulsa, Oklahoma.
- Söller, R., K. Warnke, U. Saint-Paul, and D. Blohm. 2000. Sequence divergence of mitochondrial DNA indicates cryptic biodiversity in *Octopus vulgaris* and supports the taxonomic distinctiveness of *Octopus minus* (Cephalopoda: Octopodidae). *Marine Biology* **136**: 29-35.
- Voss, G. L. and R. B. Toll. 1998. The systematic and nomenclatural status of the Octopodinae described from the Western Atlantic Ocean. In: N. A. Voss, M. Vecchione, and R. B. Toll, eds., *Systematic and Biogeography of Cephalopods*, Vol. II. Smithsonian Contributions to Zoology. Pp. 457-474.
- Warren, L. R., M. F. Schier, and D. A. Riley. 1974. Colour changes of *Octopus rubescens* during attacks on unconditioned and conditioned stimuli. *Animal Behaviour* **22**: 211-219.
- Warnke, K., R. Söller, D. Blohm, and U. Saint-Paul. 2004. A new look at geographic and phylogenetic relationships within the species group surrounding *Octopus vulgaris* Mollusca, Cephalopoda): Indications of very wide distribution from mitochondrial DNA sequences. *Journal of Zoological Systematic and Evolutionary Research* **42**: 306-312.

Submitted: 6 October 2006; **accepted:** 30 July 2007; **final corrections received:** 11 January 2008

Appendix 1. Median percentage of occurrence of the components and colors throughout the body of *Octopus insularis* within the main body patterns: % occurrence = (occurrence of the component or color in the body areas analyzed)/(total parts of body analyzed in the picture) × 100. The numbers in boldface type indicate the commonest components observed throughout the body for each body pattern.

	Components	DL-VBG	Mottle	UD	Blotch	Dymantic
Chromatic components	CR-WBE	1.6%	0.0%	0.0%	0.0%	0.0%
	CR-DBE	9.0%	12.3%	11.4%	12.8%	18.2%
	CR-RBE	0.0%	0.4%	0.0%	0.0%	3.1%
	CR-WS	15.7%	57.7%	28.4%	32.1%	9.9%
	CR-WD	4.3%	1.4%	5.4%	3.5%	0.0%
	CR-DS	0.0%	4.9%	5.3%	0.4%	0.0%
	CR-LB	14.8%	4.2%	0.6%	40.9%	6.2%
	CR-DBA	0.0%	2.3%	0.4%	2.9%	4.2%
	CR-ABE	1.9%	8.2%	6.9%	2.7%	2.6%
	CR-WV	0.5%	4.1%	3.3%	2.0%	1.3%
	CR-BH	0.0%	0.6%	0.0%	0.0%	18.8%
	CR-ABA	0.0%	19.9%	2.3%	12.2%	0.0%
	CR-PS	2.9%	4.0%	4.3%	3.0%	0.6%
	CR-BB	0.7%	11.1%	2.6%	3.4%	2.0%
	CR-BGE	8.3%	4.7%	8.0%	9.1%	18.6%
	CR-LDS	5.4%	0.0%	0.0%	0.0%	0.0%
Textural component	TE-R	32.9%	47.5%	54.2%	22.1%	29.0%
	TE-SP	9.6%	55.0%	38.3%	12.6%	5.2%
	TE-BP	0.0%	13.3%	9.8%	3.0%	0.0%
	TE-S	63.0%	36.4%	34.7%	100.1%	62.5%
	TE-T	0.0%	8.9%	7.1%	0.0%	0.0%
Colors	C-Y	22.5%	37.2%	39.7%	22.6%	6.7%
	C-R	4.9%	26.3%	32.4%	16.6%	4.2%
	C-BR	73.8%	87.8%	86.8%	91.8%	75.6%
	C-W	63.6%	74.7%	53.1%	59.6%	52.7%
	C-BG	49.2%	49.7%	20.1%	45.1%	56.0%

Appendix 2. Relationship of components, skin pattern, and colors of *Octopus insularis* with Body Patterns: % occurrence = (the times that component appeared in the pictures with a distinct body pattern)/(total of pictures analyzed with this body pattern) $\times$ 100. The numbers at the top of each column indicate the total of pictures analyzed of each body pattern, and the numbers in boldface type indicate the typical components for the *Octopus insularis*.

	Components	Blotch (11)	Mottle (22)	UD (12)	Dymantic (7)	DL-VBG (7)
Chromatic components	CR-WBE	0.00	0.00	0.00	0.00	42.86
	CR-RBE	0.00	4.55	0.00	28.57	0.00
	CR-DBE	90.00	100.00	100.00	100.00	85.71
	CR-WS	63.64	100.00	83.33	42.86	71.43
	CR-WD	9.09	9.09	33.33	42.86	40.00
	CR-DS	9.09	36.36	25.00	42.86	0.00
	CR-LB	90.91	27.27	8.33	14.29	42.86
	CR-DBA	60.00	62.50	8.33	57.14	0.00
	CR-ABE	36.36	63.64	33.33	14.29	28.57
	CR-WV	36.36	81.82	54.55	0.00	20.00
	CR-BH	0.00	4.55	0.00	71.43	0.00
	CR-ABA	54.55	81.82	16.67	0.00	0.00
	CR-PS	87.50	90.00	100.00	100.00	100.00
	CR-BB	18.18	50.00	16.67	14.29	14.29
	CR-BGE	90.91	50.00	58.33	100.00	85.71
	CR-LDS	0.00	0.00	0.00	0.00	14.29
Textural component	TE-SP	45.45	95.45	66.67	28.57	42.86
	TE-BP	9.09	50.00	41.67	0.00	0.00
	TE-T	0.00	31.82	16.67	0.00	0.00
Skin pattern	SP-RWR	No photos	100.00	100.00	100.00	100.00
	SP-AB	54.55	86.36	16.67	28.57	0.00
	SP-DS	0.00	9.09	25.00	14.29	0.00
	SP-LS	90.91	45.45	75.00	100.00	100.00
	SP-DR	63.64	36.36	100.00	85.71	28.57
	SP-LR	27.27	4.55	33.33	85.71	100.00
	SP-BL	90.91	27.27	0.00	14.29	28.57
Colors	C-Y	81.82	81.82	100.00	42.86	85.71
	C-R	72.73	95.45	91.67	42.86	85.71
	C-BR	100.00	100.00	100.00	100.00	100.00
	C-W	100.00	100.00	100.00	100.00	100.00
	C-BG	90.91	100.00	91.67	100.00	100.00
	C-BL	9.09	36.36	25.00	42.86	0.00